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Search for quantitative trait loci affecting growth and carcass traits in a cross population of beef and dairy cattle[1]

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ABSTRACT: A genome scan to detect QTL influencing growth and carcass-related traits was conducted in a Charolais × Holstein crossbred cattle population. Phenotypic measurements related to growth and carcass traits were made on the 235 second-generation crossbred males of this herd (F2 and reciprocal backcrosses), which were born in 4 consecutive annual cohorts. Traits measured in vivo were related to birth dimensions, growth rates, and ultrasound measurements of fat and muscle depth. The animals were slaughtered near a target BW of 550 kg, and a wide range of postmortem traits were measured: visual assessment of carcass conformation and carcass fatness, estimated subcutaneous fat percentage, weights of kidney knob and channel fat, and weights of carcass components after commercial and full-tissue dissections. The whole population, including grandparents, parents, and the crossbred bulls, was genotyped initially for 139 genome-wide microsatellite markers. Twenty-six additional markers were subsequently analyzed to increase marker density on some of the chromosomes where QTL had been initially identified. The linear regression analyses based on the 165 markers revealed a total of 51 significant QTL at the suggestive level, 21 of which were highly significant (F-value $\geq$9; based on the genome-wide thresholds obtained in the initial scan). A large proportion of the highly significant associations were found on chromosomes 5 and 6. The most highly significant QTL was localized between markers DIK1054 and DIK082 on chromosome 6 and explained about 20% of the phenotypic variance for the total bone proportion estimated after the commercial dissection. In the adjacent marker interval on this chromosome, 2 other highly significant QTL were found that explain about 30% of the phenotypic variance for birth dimension traits (BW and body length at birth). On chromosome 5, the most significant association influenced the lean:bone ratio at the forerib joint and was flanked by markers DIK4782 and BR2936. Other highly significant associations were detected on chromosomes 10 (estimated subcutaneous fat percentage), 11 (total saleable meat proportion), 16 (prehousing growth rate), and 22 (bone proportion at the leg joint). These results provide a useful starting point for the identification of the genes associated with traits of direct interest to the beef industry, using fine mapping or positional candidate gene approaches.

Key words: carcass composition, cattle, growth trait, quantitative trait loci

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INTRODUCTION

Heritability estimates for carcass-related traits in cattle suggest that a favorable response to selection could be achieved for these traits (reviewed by Marshall, 1999). However, the classical breeding improvement of these traits is hampered, because they can only be assessed after slaughter. The use of marker- or

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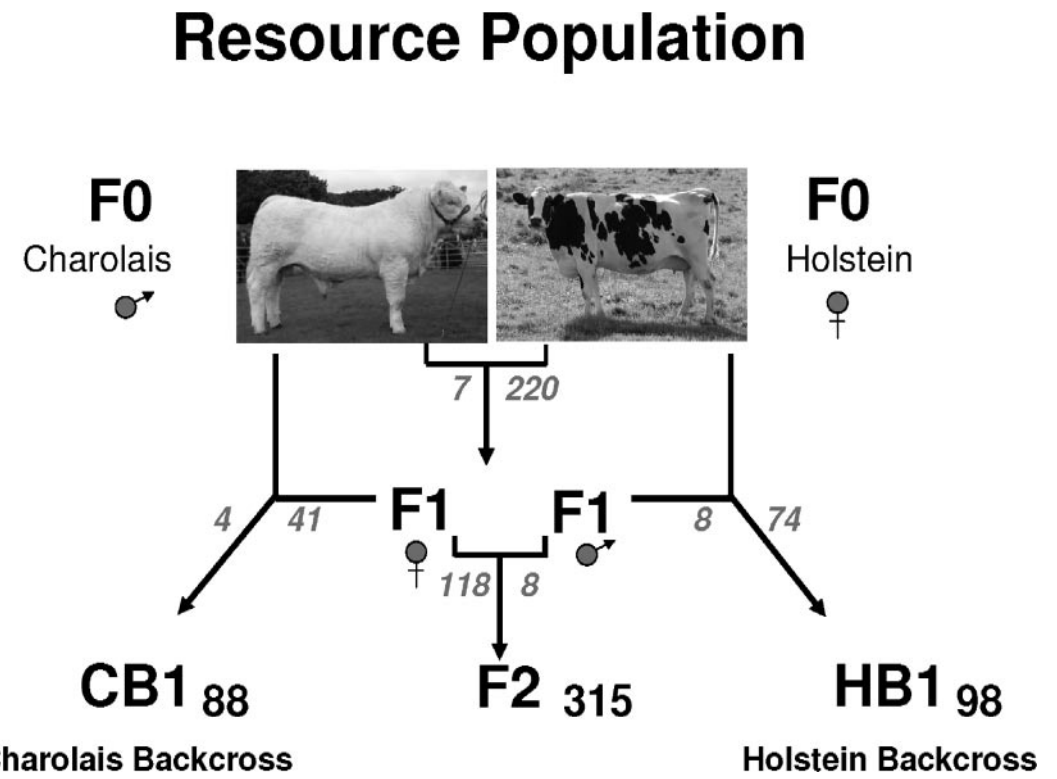

Figure 1. Structure of the Charolais × Holstein resource population used in the QTL mapping experiment described in this work. The number of founders and F1 individuals used to obtain the second-generation animals of the herd are indicated in gray small numbers. The number of F2, Holstein backcross individuals (HB1), and Charolais Backcross individuals (CB1) includes both sexes, although phenotypic data for the growth and carcass-related traits analyzed in this work were only measured in the second generation male individuals (149 F2, 45 CB1, and 41 HB1).

gene-assisted programs could easily enhance the genetic progress for these traits as well as help breeders to make choices regarding the final destination of meat products. For these promises to be realized, the identification of markers or genes associated with the variation in meat production traits is required.

The search for QTL affecting carcass yield and carcass composition in cattle has been mainly conducted by studying commercial half-sib families (Mizoshita et al., 2004; Mizoguchi et al., 2005) or experimental crosses [e.g., *Bos indicus* × *Bos taurus* (Stone et al., 1999; Casas et al., 2003) and Limousin × Wagyu cattle (Alexander et al., 2007)]. In the case of experimental cross populations, the QTL model used is based on the assumption that the founder lines are fixed for alternative alleles at the QTL (Haley et al., 1994).

The objective of the current research was to identify QTL affecting traits of direct interest to the beef industry by using an experimental cross between dairy (Holstein) and beef (Charolais) *B. taurus* breeds, through a combined F2 and backcross design. The extreme divergence of dairy and beef phenotypes in these parental breeds suggests that they may carry different alleles at loci controlling production-related traits, which enhances the statistical power of the experiment. In addition to standard growth- and carcass-related traits, the analyses reported here include measures of carcass quality determined in vivo (e.g., by ultrasound measurements of fat deposition and eye muscle depth) and more detailed trait measurements, carried out postmortem, related to carcass yield (e.g., full tissue dissection) and carcass quality (e.g., visual assessment of carcass fatness and carcass conformation).

MATERIALS AND METHODS

Studies were carried out under the United Kingdom Home Office animal experimentation license, and all procedures were inspected annually.

Resource Population and Phenotypic Measurements

A 2-generation resource population (Figure 1) was established at the Roslin Institute (UK) using 7 Charolais sires and 220 Holstein dams as founders, which were crossed to obtain 137 F1 individuals. Eight F1 sires were crossed with 118 F1 dams to obtain a total of 315 F2 individuals. The same F1 sires were also mated to 74 Holstein dams to obtain 98 Holstein backcross individuals (**HB1**). In addition, 4 of the Charolais sires were crossed to 41 F1 dams to obtain 88 Charolais backcross individuals (**CB1**). In each generation, matings between closely related individuals (half-sibs, parents-offspring) were avoided.

Phenotypic data were collected on the 235 bull calves of this second generation (149 F2, 45 CB1, and 41 HB1). Management was standardized according to standard

commercial beef practice with the aim of controlling environmental factors as far as possible. The bulls were suckled by their dams until they were approximately 6 mo of age. An exception was the HB1 bulls, which were removed from their dams at birth, because suckling by the high genetic merit Holsteins was not practical. Where possible, these bulls were fostered onto F1 cows that had given birth to heifers (who were raised as dairy calves). The others (26 in total) were raised on milk replacement and weaned at 4 wk to solid rations. At 6 mo of age, all animals were housed and fed ad libitum on a concentrate and straw regimen designed to achieve a target BW at slaughter of 550 kg at about 12 mo of age.

In Vivo-Measured Traits. The growth traits analyzed in this study were birth weight, prehousing growth rate, posthousing growth rate, body length at birth, and rate of increase in body length. The estimation of the growth rates was based on measurements taken routinely from birth until the time of slaughter. In the prehousing period, animals were weighed 6 times on average, whereas during the posthousing period, on average, 18 BW measurements were taken for each animal. For the rate of body length increase, most animals had 5 measurements taken between birth and 6 mo of age. Ultrasound scans were taken at approximately 250 d of age, which allowed measurements of eye muscle depth and fat depth at the levels of the 13th thoracic rib and third lumbar vertebra.

Carcass and Dissection-Related Traits. After commercial slaughter and dressing, the kidney knob and channel fat (**KKCF**), comprised of the perinephric and retroperitoneal fat deposits, was weighed and recorded as a percentage of HCW. Within 45 min of slaughter, HCW, external fat cover, and conformation of the carcasses were visually evaluated by trained inplant assessors following a 2-way grid, according the European Economic Community (**EEC**) Beef Carcass Classification Scheme (Commission of the European Communities, 1982). These scores (EUROP fat and EUROP conformation) were later converted to the corresponding mean classification units following the suggestions of Kempster et al. (1986b). The percentage of subcutaneous fat in the carcass was estimated visually to the nearest unit by the experienced Meat and Livestock Commission (**MLC**) technical staff (Kempster and Harrington, 1980). Measurements of pH were also recorded.

Carcass dimensions, including side length, length of hind leg, circumference of buttock, and thickness of hind leg, were measured on the hot carcass. These measurements were used to calculate 2 ratios related to carcass conformation, buttock:leg ratio and leg thickness:length ratio. After 24 h of chilling, both sides of the carcasses were quartered. The quarters of the left-hand side were shipped to the MLC experimental butchery (Milton Keynes, UK), and the right-hand side was commercially sold.

At the MLC, various measurements were made. The degree of marbling was scored on the exposed cut surface of the sirloin muscle (longissimus thoracis) at the level of the 10th rib using a standard 8-point subjective scale (with greater scores indicating greater intramuscular fat content; Kempster et al., 1986a).

Subsequently, the fore- and the hindquarters were cut into primal joints [forequarter joints: brisket, chuck, clod, forerib, Jacob's ladder, shin, sticking (neck); hindquarter joints: fillet, leg, rump, sirloin, silverside, thick flank, thin flank, topside]. Two of the primals, the forerib and the leg, were labeled, vacuumed-packed, and frozen for subsequent full-tissue dissection.

The remaining joints were prepared to obtain the retail cuts according the MLC standard retail cutting protocol for commercial dissection. The following weights were recorded: untrimmed joint, trimmed joint, lean trim, fat trim, bone trim, and other trim.

The forerib and leg joints were later defrosted and cut to retail specifications (as described above). Subsequently, they were fully dissected into the different tissues: bone (for forerib, further divided into vertebrae and other bone), subcutaneous fat, intermuscular fat, and lean tissue.

From the weights obtained by commercial dissection, the total saleable meat proportion and total bone proportion in the side were calculated. The fat removed during the commercial dissection was also calculated (fat trim proportion).

From the full-tissue dissection, the following traits were individually calculated for the forerib and the leg joints: lean proportion, intermuscular fat proportion, bone proportion, and lean:bone ratio. Basic statistics for the 26 traits analyzed in this study, grouped in 5 trait categories, are presented in Table 1.

Genotypes and Linkage Map Construction

Methods using proteinase K and phenol-chloroform were used to extract DNA from blood samples following standard protocols. The population was genotyped for a total of 165 markers, in 2 stages, as described previously by Gutiérrez-Gil et al. (2008). Initially, 139 markers that were distributed across the bovine autosomes were genotyped. After an initial QTL analysis, 26 additional markers located on chromosomes 1, 5, 6, 10, 12, 15, 16, 22, and 29 were included in the analysis with the aim of increasing marker density on chromosomes where QTL affecting sensory, growth, and carcass-related traits had been detected in the initial genome-wide analysis (see below). Marker linkage maps were built with CRIMAP version 2.4 (Green et al., 1990). The information content of the linkage maps was calculated according to Knott et al. (1998). Marker identities and genetic distances according to the sex-averaged map have previously been reported for this Charolais × Holstein cross population (Gutiérrez-Gil et al., 2008).

Table 1. Average value, SD, range, and number of animals with observation for each trait measured in the present study

Item	Trait[1]	Avg	SD	Range	Number of animals
Growth traits	BBW, kg	45.561	6.237	30–60	209
	Pre-GR, kg/d	1.256	0.269	0.27–1.71	246
	Post-GR, kg/d	1.588	0.199	1.02–2.15	241
	BBLength, mm	715.105	58.910	503–912	248
	BLengthGR, mm/d	2.942	0.597	0.79–4.76	248
Ultrasound measurements	Rib13–6, mm	2.383	1.116	0.4–5.6	225
	Lumbar3–6, mm	2.728	1.420	0.3–9	225
	Eye muscle, mm	52.750	9.371	80.2–70.8	225
General carcass traits	Subcutaneous fat estimate, %	6.660	1.529	3–10	235
	Marbling score	0.868	0.742	0–3	235
	KKCF, kg	0.014	0.003	0.01–0.02	235
	EUROP fat score	6.723	1.747	2.5–13.5	235
	EUROP conformation score	6.889	1.141	6–10	234
	Buttock:leg ratio	1.474	0.053	1.29–1.67	235
	Leg thickness:length ratio	0.358	0.019	0.25–0.41	235
Commercial dissection traits	TSaleableMP	0.657	0.020	0.57–0.70	235
	TBoneP	0.163	0.011	0.13–0.2	235
	FatTrimP	0.075	0.016	0.04–0.14	235
Full-tissue dissection traits	IMfat-prop-rib	0.133	0.022	0.08–0.21	235
	Lean-prop-rib	0.632	0.032	0.53–0.72	235
	Bone-prop-rib	0.172	0.017	0.13–0.25	235
	Lean:bone-rib	3.705	0.429	2.46–5.04	235
	IMfat-prop-leg	0.048	0.011	0.02–0.09	235
	Lean-prop-leg	0.485	0.022	0.43–0.54	235
	Bone-prop-leg	0.351	0.027	0.29–0.41	235
	Lean:bone-leg	1.394	0.158	1.04–1.85	235

[1]BBW = BW at birth; Pre-GR = prehousing growth rate; Post-GR = posthousing growth rate; BBLength = body length at birth; BLengthGR = body length growth rate; Rib13–6 = fat depth at the level of the 13th thoracic rib; Lumbar3–6 = fat depth at the level of the third lumbar vertebra; Eye muscle = eye muscle depth; Marbling score, on a 8-point scale (0 = leanest, 7 = fattest; Kempster et al. 1986a); KKCF = kidney knob and channel fat; EUROP fat score = European Economic Community (EEC) fat classes converted to the corresponding mean subcutaneous fat content estimate according to Kempster et al. (1986b); EUROP conformation score = EEC conformation classes converted to the corresponding mean classification units on a 15-point scale following Kempster et al. (1986b); Buttock:leg ratio = ratio of buttock circumference to leg length; Leg thickness:length ratio = ratio of leg thickness to leg length; TSaleableMP = sum of the weight of trimmed retail joints and lean trimmings for all the fore- and hindquarter joints as a proportion of total weight of hind- and forequarters [forequarter joints = brisket, chuck, clod, forerib, Jacob's ladder, shin, sticking (neck); hindquarter joints = fillet, leg, rump, sirloin, silverside, thick flank, thin flank, topside]; TBoneP = sum of the bone weight for all the fore- and hindquarter joints as a proportion of the total weight of hind and forequarters; FatTrimP = sum of the fat trim for all the fore- and hindquarter joints as a proportion of total weight of hind- and forequarters; IMfat-prop-rib = weight of intermuscular fat in the forerib joint as a proportion of the forerib weight after full tissue dissection; Lean-prop-rib = lean weight in the forerib joint as a proportion of the forerib weight after full tissue dissection; Bone-prop-rib = sum of weight of vertebral column and weight of other bone in the forerib joint as a proportion of forerib weight after full tissue dissection; Lean:bone-rib = ratio of lean weight to bone weight (sum of vertebral column weight and other bone in forerib weight) in the forerib joint; IMfat-prop-leg = weight of intermuscular fat in the leg joint as a proportion of the leg weight after full tissue dissection; Lean-prop-leg = lean weight in the leg joint as a proportion of the leg weight after full tissue dissection; Bone-prop-leg = bone weight in the leg joint as a proportion of the leg weight after full tissue dissection; Lean:bone-leg = ratio of lean weight to bone weight in the leg joint.

Statistical Analysis

Initial Genome Scan. Initially an analysis was carried out using the 139 markers by fitting a single-QTL model at 1-cM intervals along each chromosome according to the least squares method described by Haley et al. (1994) and implemented by the Web-based QTL Express software (Seaton et al., 2002). For all traits, genetic composition (F2, CB1, HB1) and cohort were included as fixed factors in the linear model. For the growth-related traits (prehousing growth rate, posthousing growth rate, body length growth rate, Table 1), differences in early feeding between some of the HB1 and the rest of the population were taken into account by including the early feeding variable as a fixed factor in the QTL model.

The fraction of the phenotypic variance explained by the QTL was determined as the percentage reduction in the residual variance due to the inclusion of the QTL in the model (adapted from Knott et al., 1996). A10,000-permutation test was performed to establish 5 and 1% chromosome-wide thresholds (Churchill and Doerge, 1994). Genome-wide *P*-values were defined according to de Koning et al. (2001) by taking into account the length of each chromosome where a QTL was located.

Increasing Marker Density at QTL Regions. A second analysis was performed for the 9 chromosomes where additional microsatellite markers had been added. Because these markers were not selected at random, genome-wide *P*-values were not recalculated. Instead, the 5 and 1% genome-wide thresholds obtained using the first marker set, which corresponded to *F*-ratios of approximately 8.5 and 10.5, respectively, were used to identify significant associations. Hence a QTL with a statistical *F*-value $\geq$9 is referred to as highly significant. Using the 165-marker linkage map, bootstrap

95% confidence intervals (**95% CI**) were estimated as described by Visscher et al. (1996).

2-QTL Model. Where evidence was found for a single QTL on a chromosome, the presence of a second QTL was investigated. The best 2-linked-QTL model was identified by a grid search at 1 cM resolution of all possible positions for 2 QTL. The best-fitting model with 2 QTL (denoting the residual sum squares as RSS2 and degree of freedom as df2) was tested against the best model fitting 1 QTL (denoting the residual sum squares as RSS1 and degree of freedom as df1) using an *F*-test. The *F*-ratio was calculated by [(RSS1 − RSS2)/(df1 − df2)]/[RSS2/df2] with (df1 − df2) degrees of freedom in the numerator, considering additive and dominance effects in the genetic model. The 2-QTL model was accepted if there was a significant improvement over the best 1-QTL model at $P < 0.05$.

Sire Interaction. To test whether the founder lines were fixed for alternative alleles at the QTL identified, the possibility of an interaction between the sires and the QTL was tested. Because this analysis could not distinguish between the differences in genetic composition of the F1 sires and the Charolais founders, the backcross individuals were removed from the analysis to avoid bias. Subsequently, the phenotypic data from the F2 individuals were reanalyzed by replacing the breed composition factor with sire, and fitting the interaction between the QTL and sire into the genetic model, considering only additive effects. The model including the breed interaction was tested against the best model with no interaction using an *F*-test, as described above. The model with interactions was accepted if the *F*-value reached the 5% significance level with (df1 − df2) degrees of freedom.

RESULTS

Overall QTL Analysis Results

The average marker information content across the genome was 0.60 (Gutiérrez-Gil et al., 2008). Using the genotypic information derived from the 165 markers, the regression analysis for the 26 tested traits revealed a total of 51 significant QTL at the suggestive significance level, which for the bovine genome corresponds to a chromosome-wide *P*-value <0.034 (Lander and Kruglyak, 1995). The significant associations were located on 13 of the 29 bovine autosomes, with a large proportion of QTL found on chromosomes 6 (16 significant QTL) and 5 (7 significant QTL). Chromosomes 16 and 22 also harbored a substantial number of the significant QTL (with 6 and 5 significant QTL, respectively). Twenty out of the 51 QTL showed *F*-values ≥9 and were considered as highly significant. A detailed characterization of the significant QTL identified is summarized in Table 2.

Of the 51 QTL, 7 were associated with growth and birth dimension traits (chromosomes 6, 8, 16, 26) and 3 had effects on ultrasound measurements (chromosomes 6, 11). Four of these trait-chromosome combinations affecting the traits measured in vivo were highly significant and influenced the lumbar fat depth ultrasound measurement, birth weight and birth body length (chromosome 6), and pregrowth rate (chromosome 16). The remaining significant associations showed effects on the postmortem traits: dissection (30 QTL) or carcass-related traits (11 QTL), with 16 of these postmortem-related QTL being highly significant. The percentage of the phenotypic variance due to the QTL effect ranged between 4.8% (for the QTL affecting leg lean proportion on chromosome 5) and 36% (for the QTL influencing bone proportion at the leg on chromosome 6). Because the average number of progeny per family was small, sampling bias may have led to the overestimation of the QTL effects (Göring et al., 2001).

The 95% CI intervals for the highly significant QTL ranged between 16.5 and 72.5 cM in length (Table 2). As expected, the shortest 95% CI was obtained for the QTL that showed the greatest statistical support (influencing total bone proportion on chromosome 6). For the suggestive QTL, the 95% CI covered most of the length of the chromosome (data not shown).

The 9 trait-chromosome combinations for which the 2-QTL model gave significantly better fit than the single QTL ($P < 0.05$) are shown in Table 3, together with the most likely positions and sizes of the effects of the 2 suggested QTL.

The sire interaction was only significant for 3 of the significant QTL, those affecting leg bone proportion on chromosome 4, and total saleable meat proportion and leg lean proportion on chromosome 5. Only 2, 1, and 3 sire families, respectively, appeared to be segregating for these QTL. For the remaining QTL, the evidence suggests that 2 alleles were segregating in all families.

Chromosome 6

Under the 1-QTL model including only additive and dominance effects, the greatest number of significant associations detected in this study was found on chromosome 6. These were 16 QTL that influenced all trait groups studied: growth and ultrasound measurements, fat carcass-related traits, and dissection traits (Table 2). Twelve of these QTL were highly significant and were located in the region between 37 and 56 cM of the linkage map for this chromosome (BM1329-DIK1054-DIK82; Figure 2). The first marker interval included in this region, [BM1329-DIK1054], contained QTL for growth and fat carcass-related traits, whereas the remaining QTL affecting dissection-related traits (full tissue and commercial dissection) were localized into the next marker interval [DIK1054-DIK82]. The most highly significant QTL identified on chromosome 6 affected total bone proportion at 51 cM (95% CI = 38.5 to 55 cM) and was accompanied by effects on other traits influenced by or correlated with bone weight

(e.g., the bone proportion at the forerib and leg joints, the lean:bone ratio at the forerib and leg joints, fat trim proportion).

All the QTL detected on chromosome 6 showed clear additive modes of action (only the one for the forerib lean:bone ratio showed partial dominance effects). For the highly significant QTL identified on this chromosome, the size of the additive effect expressed in phenotypic SD units of the trait ranged from 0.43 for the lumbar fat depth (44 cM) to 0.83 for the EUROP fat score (37 cM). For the QTL influencing dimensions at birth (birth weight and birth body length, at 38 to 39 cM) and the bone proportion-related traits (total bone proportion and leg bone proportion, at 51 to 52 cM), the QTL explained approximately 20 and 36% of the phenotypic variance, respectively. Considering the signs of the additive effects, the Charolais alleles for the QTL identified in the [BM1329-DIK1054-DIK82] region were associated with greater BW and body length at birth and increased bone proportion in the commercial and full-tissue dissections, affecting both the fore- and hindquarters.

Quantitative trait loci on this chromosome for traits related to fat deposition (KKCF, lumbar fat depth, es-

Table 2. Characterization of the QTL effects exceeding the suggestive significance level (chromosome-wide *P*-value <0.034; Lander and Kruglyak, 1995) in the Holstein × Charolais cross population analyzed in the present study for growth traits (Growth), ultrasound measurements (Ultras. M), general carcass traits (Carcass), commercial dissection traits (CommDiss), and full-tissue dissection traits (Diss)

Chr[1]	Trait[2]	*F*-value[3]	cM (95% CI)[4]	Flanking interval[5]	p_c[6]	*a*[7]	*d*[7]	V[8]
1	Buttock:leg (Carcass)	6.72	81	INRA128-BM864	0.0105	0.01	0.03***	5.6
2	Lean:bone-rib (Diss)	7.08	124	**IDVGA2**	0.0083	2.50	−23.24***	5.9
4	Lean:bone-leg (Diss)	6.3	33	BMS1788-MAF50	0.0161	−0.08**	−0.082	5.28
	Bone-prop-leg (Diss)	8.52	33	BMS1788-MAF50	0.0019	0.01**	0.02*	7.02
5	TSaleableMP (CommDiss)	**10.86**	24 (9 to 68)	RM103-BM321	0.0001	−0.01***	0.005	8.79
	Lean-prop-rib (Diss)	**9.28**	29 (2.5 to 65.5)	RM103-**BM321**-DIK4782	0.0011	−0.01***	0.001	7.6
	Bone-prop-rib (Diss)	**14.51**	40 (37 to 66.5)	DIK4782-BR2936	<0.0001	0.01***	−0.001	11.37
	Buttock:leg (Carcass)	8.61	40		0.002	−0.02***	0.003	7.08
	TBoneP (CommDiss)	7.98	41		0.0264	0.005***	0.0007	6.37
	Lean:bone-rib (Diss)	**20.99**	42 (34 to 66)		<0.0001	−0.27***	0.008	15.66
	Lean-prop-leg (Diss)	5.72	116	ETH152	0.03	−0.01**	0.005	4.80
6	IMfat-prop-leg (Diss)	5.66	0	DIK5076	0.0323	0.003**	−0.0028	7.41
	EUROP fat score (Carcass)	**11.21**	37 (28.5 to 61.5)	BM1329-DIK1054	0.0003	0.95***	0.23	9.02
	BBLength (Growth)	**16.38**	38 (23 to 60.5)		<0.0001	−30.51***	12.17	29.05
	BBW (Growth)	**15.27**	39 (27 to 65)		<0.0001	−3.59***	0.61	27.19
	KKCF (Carcass)	**13.35**	43 (35 to 83)		<0.0001	0.002***	−0.0002	10.53
	Lumbar3–6 (Ultras. M)	**10.21**	44 (35 to 91)		0.0009	0.61***	0.11	18.83
	FatTrimP (CommDiss)	**13.93**	46 (34 to 66)	DIK1054-DIK82	<0.0001	0.01***	−0.002	10.87
	IMfat-prop-rib (Diss)	6.31	48 (32–133)		0.0198	0.01***	−0.008	5.27
	TBoneP (CommDiss)	**29.89**	51 (38.5 to 55)		<0.0001	−0.008***	−7.0E-4	21.12
	Lean-prop-leg (Diss)	**11.47**	52 (17.5 to 77.5)		0.0002	0.01***	0.003	16.85
	Bone-prop-leg (Diss)	**23.58**	52 (22.5 to 60)		<0.0001	−0.02***	−0.005	36.05
	Lean:bone-leg (Diss)	**21.12**	52 (20 to 60.5)		<0.0001	0.11***	0.03	0.024
	Bone-prop-rib (Diss)	**23.5**	53 (37 to 56)		<0.0001	−0.01***	0.004	17.22
	Subcutaneous fat estimate (Carcass)	7.25	53		0.0091	0.63***	0.44	6.43
	Lean:bone-rib (Diss)	**15.13**	56 (40.5 to 61)		<0.0001	0.21***	−0.12*	11.81
	Rib13–6 (Ultras. M)	6.82	76	DIK2320-CSN3	0.0128	0.32***	−0.08	12.95
8	BBW (Growth)	8.05	19	IDVGA11-**DIK106**-HUJ174	0.0033	−2.34***	−0.86	15.17
	BBLength (Growth)	5.49	28	DIK106-HUJ174	0.029	−17.64**	−13.91	10.3
9	Bone-prop-leg (Diss)	5.14	12	ETH225-BM2504	0.0309	−0.008*	0.01*	9.29
10	FatTrimP (CommDiss)	6.72	12	DIK5169-BMS528	0.0179	−0.005*	−0.008*	5.53
	Subcutaneous fat estimate (Carcass)	**9.62**	37 (0 to 72.5)	BMS528-TGLA378	0.0008	−0.83***	−0.32	8.36
	EUROP fat score (Carcass)	7.3	61	TGLA378-BM888	0.01	−0.5*	−0.83**	6.06
	Lean-prop-rib (Diss)	6.06	61		0.0237	0.01**	0.009	5.11
11	Lumbar3–6 (Ultras. M)	6.91	5	BM716-INRA177	0.0081	−0.20	−0.87***	13.10
	TSaleableMP (CommDiss)	**9.03**	63 (63 to 89)	ILSTS100-**IDVGA3**-HUJV174	0.0012	−0.01***	0.002	15.75
	Bone-prop-leg (Diss)	5.33	89	HUJV174-**BMS607**	0.0321	0.007*	0.009*	9.57
	TBoneP (CommDiss)	6.45	89		0.0108	0.004***	0.002	13
16	BBLength (Growth)	5.5	0	**BM121**	0.0252	−14.86*	−12.36	10.60
	Bone-prop-leg (Diss)	6	29	ETH11-BM719	0.0179	0.01**	−0.007	5.01
	Pre-GR (Growth) (early feeding factor)	**9.73**	47	ETH11-BM719	0.0014	0.05	−0.13***	18.14
	Buttock:leg (Carcass)	8.17	85	HUJ625-DIK4011	0.0022	−0.02***	0.009	6.74
	EUROP conformation score (Carcass)	5.27	87	HUJ625-**DIK4011**	0.0311	−0.68**	−0.21	10.15
	TBoneP (CommDiss)	7.72	87	HUJ625-**DIK4011**	0.0041	0.006***	−0.001	6.37
19	Marbeling (Carcass)	7.03	18	HEL10-BMS2142	0.0061	−0.36***	0.13	6.25

Continued

Table 2 (Continued). Characterization of the QTL effects exceeding the suggestive significance level (chromosome-wide *P*-value <0.034; Lander and Kruglyak, 1995) in the Holstein × Charolais cross population analyzed in the present study for growth traits (Growth), ultrasound measurements (Ultras. M), general carcass traits (Carcass), commercial dissection traits (CommDiss), and full-tissue dissection traits (Diss)

Chr[1]	Trait[2]	*F*-value[3]	cM (95% CI)[4]	Flanking interval[5]	p_c[6]	*a*[7]	*d*[7]	V[8]
22	Marbeling (Carcass)	6.52	32	BM3406-BM3628	0.0122	−0.31***	0.16	5.82
	FatTrimP (CommDiss)	5.86	49	BM3628-**DIK2443**-HAUT24	0.0211	−0.006***	−0.0008	4.94
	TBoneP (CommDiss)	8.69	53	DIK2443-HAUT24	0.0025	0.005***	−0.001	7.17
	Lean:bone-leg (Diss)	7.3	55		0.0074	−0.07***	0.02	6.07
	Bone-prop-leg (Diss)	**9.66**	56 (41 to 74)		0.0007	0.01***	−0.005	7.89
26	Post-GR (Growth)	4.84	28	HEL11-**RM26**-IOBT730	0.0299	0.03	−0.08**	9.37

[1]Chr = chromosome number. For those chromosomes where additional markers were added (chromosomes in bold caps), the results from the second analysis are given.

[2]Buttock:leg ratio = ratio of buttock circumference to leg length; Lean:bone-rib = ratio of lean weight to bone weight (sum of vertebral column weight and other bone in forerib weight) in the forerib joint; Lean:bone-leg = ratio of lean weight to bone weight in the leg joint; Bone-prop-rib = sum of weight of vertebral column and weight of other bone in the forerib joint as a proportion of forerib weight after full tissue dissection; TSaleableMP = sum of the weight of trimmed retail joints and lean trimmings for all the fore- and hindquarter joints as a proportion of total weight of hind- and forequarters [forequarter joints = brisket, chuck, clod, forerib, Jacob's ladder, shin, sticking (neck); hindquarter joints = fillet, leg, rump, sirloin, silverside, thick flank, thin flank, topside]; Lean-prop-rib = lean weight in the forerib joint as a proportion of the forerib weight after full tissue dissection; Bone-prop-rib = sum of weight of vertebral column and weight of other bone in the forerib joint as a proportion of forerib weight after full tissue dissection; TBoneP = sum of the bone weight for all the fore- and hindquarter joints as a proportion of the total weight of hind and forequarters; Lean-prop-leg = lean weight in the leg joint as a proportion of the leg weight after full tissue dissection; IMfat-prop-leg = weight of intermuscular fat in the leg joint as a proportion of the leg weight after full tissue dissection; EUROP fat score = European Economic Community (EEC) fat classes converted to the corresponding mean subcutaneous fat content estimate according to Kempster et al. (1986b); BBLength = body length at birth; BBW = BW at birth; KKCF = kidney knob and channel fat; Lumbar3–6 = fat depth at the level of the third lumbar vertebra; FatTrimP = sum of the fat trim for all the fore- and hindquarter joints as a proportion of total weight of hind- and forequarters; IMfat-prop-rib = weight of intermuscular fat in the forerib joint as a proportion of the forerib weight after full tissue dissection; Rib13–6 = fat depth at the level of the 13th thoracic rib; Pre-GR = prehousing growth rate; EUROP conformation score = EEC conformation classes converted to the corresponding mean classification units on a 15-point scale following Kempster et al. (1986b); Post-GR = posthousing growth rate.

[3]Maximum *F*-statistic value for the chromosome. Based on the genome-wide thresholds obtained for the preliminary scan, those associations with *F*-value ≥9.0 (in bold) were considered as highly significant.

[4]cM = relative position in Kosambi centimorgans, from the beginning of the sex-averaged linkage map, for the maximum *F*-statistic value in the chromosome; 95% CI = 95% confidence interval obtained by bootstrapping analysis (Visscher et al., 1996) is shown for those associations with *F*-value ≥9.0.

[5]Markers flanking the position of the maximum *F*-statistic. Markers in bold caps are <1 cM from the maximum F-statistic.

[6]p_c value = chromosome-wide *P*-value obtained by permutation test for that position (Churchill and Doerge, 1994).

[7]Additive (*a*) and dominance (*d*) effects, respectively (in units of the trait); significance level: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. $a > 0$ = Holstein allele is associated with greater values of the trait; $a < 0$ = Charolais allele is associated with greater values of the trait. Same sign of *a* and *d* = dominance of the Holstein allele; opposite sign of *a* and *d* = dominance of the Charolais allele.

[8]Percentage of variance explained by the QTL (adapted from Knott et al., 1996).

timated subcutaneous fat percentage, and EUROP fat score) showed large levels of significance in the same region as the QTL for growth and dissection traits described previously. However, in contrast to the results for the growth and dissection traits, the 2-QTL analysis for 3 of these fat deposition-related traits was significantly better than the 1-QTL analysis (the only exception was EUROP fat score; Table 3).

Chromosome 5

On chromosome 5, four highly significant QTL were identified (Table 2, Figure 3). Two affecting forerib lean proportion and total saleable meat proportion were localized on the first third of the chromosome, in the marker interval [RM103-BM321], although their 95% CI spanned a large proportion of the chromosome length. For these 2 QTL, the Charolais allele was associated with a greater forerib lean proportion and an increased yield of saleable meat. The 2 other highly significant QTL on this chromosome influenced the forerib bone proportion and the forerib lean:bone ratio and were located in the next marker interval, [DIK4782-BR2936], with their 95% CI covering a region of about 30 cM. This QTL region also contained suggestive QTL for the buttock:leg ratio and the total bone proportion. On this chromosome, all the QTL showed significant additive effects and no significant dominance effects. The size of the QTL effects was greater than 0.5 phenotypic SD for the QTL affecting total saleable meat proportion, forerib bone proportion, and the forerib lean:bone ratio. The percentage of the phenotypic variance explained by the highly significant QTL detected in chromosome 5 ranged from 7.6% (for the forerib lean proportion) to 15.66% (for the forerib lean:bone ratio). The 2-QTL analysis was significant for the forerib bone proportion (at 21 and 40 cM) and the leg lean proportion (at 47 and 116 cM; Table 3).

Other Chromosomes

Four additional highly significant QTL were identified on chromosomes 10 (estimated subcutaneous fat percentage), 11 (total saleable meat proportion), 16 (prehousing growth rate), and 22 (leg bone proportion; Table 2). With the exception of the QTL on chromo-

Table 3. Results for 2-QTL models that gave a significantly better fit to the data at a 5% nominal level than the equivalent single-QTL model

		F-value (4 df)[3]	F-value (2 df)[3]	QTL A[4]			QTL B[4]		
Chr[1]	Trait[2]	(2 QTL vs. 0 QTL)	2 QTL vs. 1 QTL)	Position, cM	a	d	Position, cM	a	d
2	Lean:bone-rib	6.35	5.36	44	0.04	0.23***	124	0.03	−0.25**
5	Bone-prop-rib	9.81	4.63	21	−0.01**	0.01	40	0.02***	−0.01
	Lean-prop-leg	4.95	4.03	47	−0.01**	0.001	116	−0.01**	0.004
6	EUROP fat score	6.35	5.09	54	0.75***	0.50**	133	−0.62***	−0.08
	KKCF	9.91	5.82	42	0.002***	−0.0001	132	−0.001***	0
	Lumbar3–6	8.59	6.48	0	−0.53***	−0.20	37	0.92***	0.23
10	Lean-prop-rib	5.14	4.04	54	0.02	−0.23**	55	−0.01	0.24**
11	TSaleableMP	6.23	3.24	73	−0.18***	−0.06	74	0.17***	0.06
16	EUROP conformation score	5.55	5.61	12	0.05	−0.70***	87	−0.75***	−0.25

[1]Chr = chromosome number.

[2]Lean:bone-rib = ratio of lean weight to bone weight (sum of vertebral column weight and other bone in forerib weight) in the forerib joint; Bone-prop-rib = sum of weight of vertebral column and weight of other bone in the forerib joint as a proportion of forerib weight after full tissue dissection; Lean-prop-leg = lean weight in the leg joint as a proportion of the leg weight after full tissue dissection; EUROP fat score = European Economic Community (EEC) fat classes converted to the corresponding mean subcutaneous fat content estimate according to Kempster et al. (1986b); KKCF = kidney knob and channel fat; Lumbar3–6 = fat depth at the level of the third lumbar vertebra; Lean-prop-rib = lean weight in the forerib joint as a proportion of the forerib weight after full tissue dissection; TSaleableMP = sum of the weight of trimmed retail joints and lean trimmings for all the fore- and hindquarter joints as a proportion of total weight of hind- and forequarters [forequarter joints = brisket, chuck, clod, forerib, Jacob's ladder, shin, sticking (neck); hindquarter joints = fillet, leg, rump, sirloin, silverside, thick flank, thin flank, topside]; EUROP conformation score = EEC conformation classes converted to the corresponding mean classification units on a 15-point scale following Kempster et al. (1986b).

[3]F-statistic value obtained when the best model fitting 2 QTL was tested against the best model fitting 0 or 1 QTL, respectively.

[4]Position (Kosambi cM) and effects in units of the trait (a = additive effect; d = dominance effect) are indicated for the first and second QTL suggested by the 2-QTL analysis (QTL A and B, respectively). Significance level for additive and dominance effects: $^{**}P < 0.01$; $^{***}P < 0.001$.

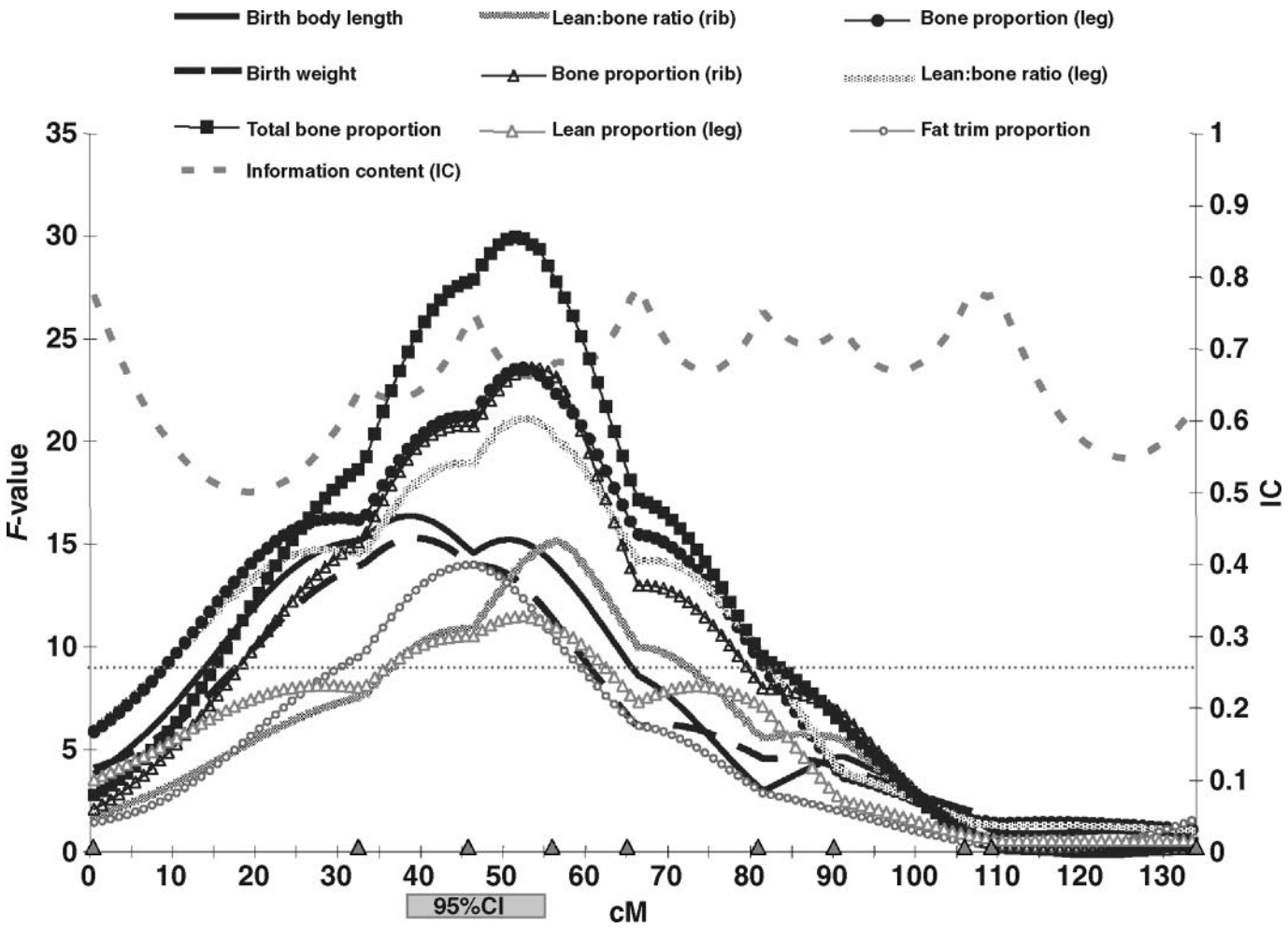

Figure 2. Highly significant QTL identified on chromosome 6 (F-value: ≥9). The F-statistic is plotted against the relative position in centimorgans. Marker information content (IC) is shown as a dashed line on the right y-axis. The dashed horizontal line indicates the threshold for a highly significant result applied in this study (F-value: ≥9). Beginning at the centromeric end, the triangles on the x-axis indicate the relative position of the markers, which were DIK5076, BM1329, DIK1054, DIK82, DIK2320, CSN3, BP7, DIK1180, BMS739, and BM2320. The 95% confidence interval (95%CI) for the most significant association identified on this chromosome, the total bone proportion after commercial dissection, is indicated with a narrow box on the x-axis.

some 16, which had significant dominance effects, these QTL showed an additive mode of inheritance and additive effects of approximately 0.5 phenotypic SD units. For the highly significant QTL detected on chromosome 10 and chromosome 11, the Charolais allele was associated with an increased fatness level and an increased saleable meat proportion, respectively. The Holstein allele was associated with an increased bone proportion for the leg bone proportion QTL found on chromosome 22. Details regarding the mode of inheritance and magnitude of the effect for the rest of the identified QTL can be found in Table 2.

DISCUSSION

This study addressed the identification of QTL influencing carcass- and dissection-related traits that are of importance to the beef industry (e.g., fatness, conformation score, and meat yield), as well as QTL for growth traits and in vivo fat and muscle depth measurements. Recognizing that there is greater power to detect QTL where the founder populations are fixed for divergent alleles, the Charolais × Holstein crossbred resource herd developed in this study should offer a high statistical power for detection of QTL affecting traits for which the 2 founder breeds have been divergently selected. For several of the carcass composition and body measurement traits for which very high significant QTL were identified in this study, this appears to be the case. The lack of significant interactions between sire and QTL for most of the significant associations is consistent with the assumption of alternative alleles being present in the founder animals from the 2 parental lines. However, there may also be within-breed segregation at these loci that is not represented in the selected founder animals or alleles segregating between sires that do not differ substantially in their effects and therefore are difficult to detect with the QTL × sire interaction analysis. Although fixed differences between beef and dairy breeds may not be directly exploited by the part of the beef industry dealing with purebreds, which is more concerned with variation segregating

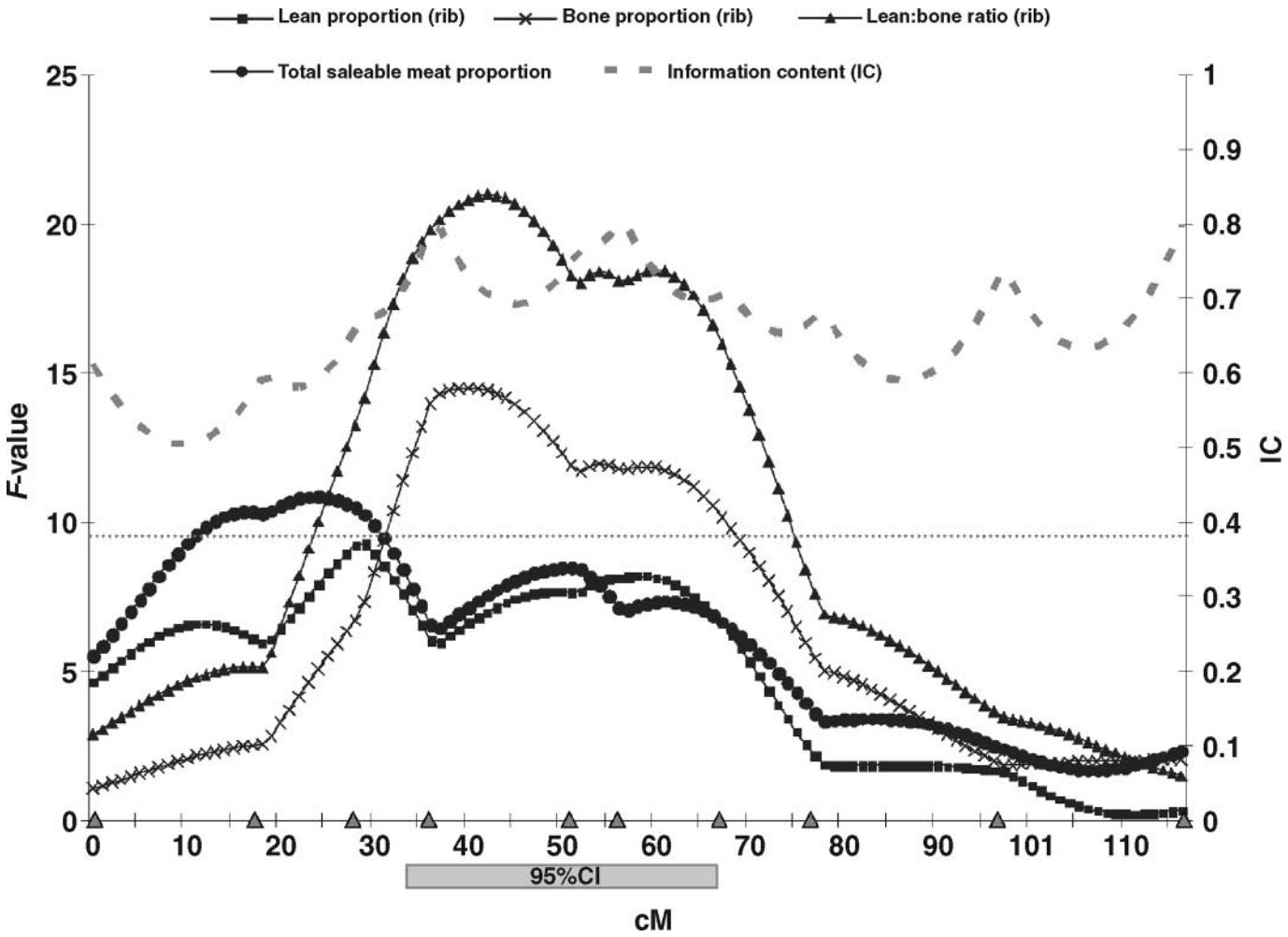

Figure 3. Highly significant *F*-statistic profiles on chromosome 5 (*F*-value: ≥9). The *F*-statistic is plotted against the relative position in centimorgans. Marker information content (IC) is shown as a dashed line on the right y-axis. The dashed horizontal line indicates the highly significant threshold considered in this study (*F*-value: ≥9). Beginning at the centromeric end, the triangles on the x-axis indicate the relative position of the markers, which were BM6026, RM103, BM321, DIK4782, BR2936, ETH10, IGF-1, DIK5104, ILSTS034, and ETH152. The 95% confidence interval (95%CI) for the most significant association identified on this chromosome, the lean:bone ratio at the forerib joint, is indicated with a narrow box on the x-axis.

within breeds, they could have a direct application to the terminal crosses to beef bulls performed in dairy herds (Wolfová et al., 2007). The use of experimental crosses also increases the chances of identifying QTL, which helps to build up knowledge of the genetic control of phenotypic variation and serves as the starting point for identifying the genes that have a direct effect on traits of economical interest. This information provides the basic knowledge to guide the search for allelic variants, which may be segregating within other populations.

Additional analyses not described in this paper involved the inclusion in the statistical model of a parent-of-origin effect, in addition to the additive and dominance effects, to test for evidence of imprinted QTL effects. However, the structure of the population comprising a mixture of backcrosses and F2 animals is not conducive to estimation of imprinting effects. Hence, our analyses of imprinting, using only the F2 animals, are less reliable than the estimates of additive and dominance effects, because they are based on a decreased set of animals, and therefore, we present here the more robust additive and dominance estimates.

Several highly significant QTL were identified in the same region of chromosome 6, covering markers BM1329-DIK1054-DIK82. The most significant effects involved dissection traits related to the proportion of bone in the carcass (total bone proportion and leg bone proportion) and were accompanied by effects on other carcass components (e.g., total fat trim proportion, leg lean proportion). In addition, 2 highly significant QTL for dimensions at birth (birth weight and body length at birth) were near the carcass-related QTL, 10 cM closer to the centromere. To better understand the nature of the significant QTL identified in this chromosome, regression analysis was performed on the individual terms comprising the ratio and proportion traits initially considered (results not shown). This exploratory analysis showed that when the separate components (bone, fat, and lean weights) of the derived dissection-related traits were analyzed individually, the greatest significance levels were for vertebral bone weight and

leg bone weight, with only 1 suggestive effect for forerib intramuscular fat weight and none for lean weight. This supports the hypothesis that the significant associations for dissection traits identified on this chromosome are likely to be the result of QTL primarily affecting bone weight.

It is also possible that the effects found on chromosome 6 for birth dimensions derive from the effects on bone proportion in the calf. The additive effects of the QTL for birth dimensions are consistent with the presence of a single QTL with effects on the 2 traits, where the Charolais allele increases animal dimensions at birth as well as carcass bone proportion. However, the possibility of 2 closely linked QTL affecting different traits cannot be discounted. The existence of multiple allelic variants at the same locus might also explain this observation.

Highly significant QTL for fat deposition-related traits (EUROP fat score, estimated subcutaneous fat percentage, KKCF, and lumbar fat depth) were also identified at the region 37 to 53 cM of chromosome 6. Although additional studies are required to understand the relationship of these associations with the other QTL detected on chromosome 6, it is noteworthy that the 2-QTL model explained the data better than the single-QTL model for KKCF, lumbar fat depth, and estimated subcutaneous fat percentage. This suggests that more than one locus is responsible for these fat-related effects. The greater degree of fatness associated with the Holstein allele at these QTL is consistent with the findings of Pfuhl et al. (2007), who showed that Charolais bulls have a decreased percentage of subcutaneous fat and decreased weights of internal fat deposits (e.g., gut, omental, kidney, and scrotum fat) than Holstein bulls.

Several QTL with effects on growth and meat production traits have previously been reported in the same region of chromosome 6 (the marker interval BM1329-DIK1054-DIK82) where many of the QTL reported here were found. In agreement with our results, the published growth-related QTL mainly occur in the centromeric section of that region (between markers BM1329 and DIK1054) and involve birth weight (Davis et al., 1998; Casas et al., 2000; Kneeland et al., 2004) and ADG (Kim et al., 2003; Kneeland et al., 2004), whereas published QTL associated with carcass yield and carcass composition have been localized closer to the middle of the chromosome [e.g., QTL affecting LM area, HCW (Casas et al., 2000), and rib thickness (Mizoguchi et al., 2005)]. The simultaneous analysis of birth weight and detailed dissection variables presented here may help to explain the relationship between QTL regions identified in the different cattle populations and correlated effects on these different traits. Hence, this is the first study suggesting that the QTL identified on this chromosome for size at birth are due to an increased bone percentage of the animal early in life. Genes in the QTL region related to bone development and bone metabolism therefore become strong candidates for this QTL (see below).

The QTL for birth weight on chromosome 6, which explained about 30% of the phenotypic variance of the trait, is of particular interest regarding dystocia and calving difficulties, which are frequently observed when sires of highly specialized beef breeds, such as Charolais or Limousin, are crossed with dairy dams. Several QTL in the same chromosomal region have been reported for calving ease and stillbirth rate (Schrooten et al., 2000; Kühn et al., 2003).

The bone component of Charolais carcasses is known to be greater than for Holstein, although unlike the QTL effects on this chromosome, Charolais cattle generally have a decreased bone percentage than Holsteins due to their greater meat component (Istasse et al., 1990; Pfuhl et al., 2007). Although the highly significant QTL we identified on chromosome 6 appear to have alternate alleles in the founder lines, it should be noted that QTL for stature and body conformation have also been reported on this chromosomal region for Holstein cows (Hiendleder et al., 2003), suggesting that alleles at this QTL may also be segregating within some cattle breeds.

The confidence interval for the QTL affecting total bone proportion on chromosome 6 contains several well-characterized genes. Among these positional candidates, the secreted phosphoprotein 1 (***SPP1***), integrin-binding sialoprotein (***IBSP***), and the matrix extracellular phosphoglycoprotein (***MEPE***) genes form a cluster of genes coding for bone-tooth mineral extracellular matrix phosphoglycoproteins and appear as strong functional candidates for the growth and bone-related QTL found in that region. In particular, the *SPP1* gene has been found to be associated with birth weight and early growth rate (Allan et al., 2007; White et al., 2007). The peroxisome proliferator-activated receptor γ, coactivator 1 α gene (***PPARGC1A***), located at the distal end of the bone-related QTL confidence interval, has been associated with back fatness in pigs (Jacobs et al., 2006) and milk fat synthesis in dairy cattle (Weikard et al., 2005). It also serves as co-activator for vitamin D receptor (Savkur et al., 2005), which is directly involved in bone metabolism. Further genetic analysis of our resource population may help to reveal whether one or more of these candidate genes is responsible for the carcass-related QTL identified in several studies.

On chromosome 5, the QTL with the greatest significance level influenced the lean:bone ratio at the rib level (41 cM). The exploratory analysis for the separate component measurements of this trait revealed significant effects for both lean and bone components, although at a decreased significance level than obtained for the ratio trait (results not shown). This exploratory analysis also suggested that the bimodal shape of the statistical profile of the lean:bone ratio may be due to the effects of 2 different QTL influencing vertebral bone weight (36 cM) and other bone weight at the forerib joint (64

cM). The lean:bone ratio QTL was accompanied by significant effects for correlated traits such as forerib bone proportion, for which evidence of 2 QTL segregating in the population was found at 21 and 40 cM. The first of these positions is close to 2 other highly significant QTL detected on this chromosome for total saleable meat and rib lean proportion. For the QTL identified on this chromosome, the Charolais allele is associated with increased lean and saleable meat proportions and decreased bone proportion compared with the Holstein allele, which agrees with general comparisons between these 2 cattle breeds (Pfuhl et al., 2007).

These results suggest that different regions of bovine chromosome 5 influence carcass composition traits, which is consistent with information reported by other authors. The interval flanked by markers DIK4782 and IGF-1 harbors QTL reported for carcass yield (Mizoshita et al., 2004), fat depth and retail product yield (Casas et al., 2000), dressing percentage (Stone et al., 1999; MacNeil and Grosz, 2002), and rib bone and fat (Stone et al., 1999). Quantitative trait loci for growth-related traits have also been identified in this chromosomal region (Davis et al., 1998; Stone et al., 1999; Kim et al., 2003; Machado et al., 2003). Quantitative trait loci affecting LM area (Casas et al., 2003) and dressing percentage (Stone et al., 1999) are also coincident with the QTL we found upstream of DIK4782 for total saleable meat proportion and rib lean proportion.

Several other QTL detected in the present study also showed a possible correspondence with QTL reported in other studies. Among the highly significant associations, the QTL affecting total saleable meat proportion on chromosome 11 overlaps with a QTL for Yield grade (Casas et al., 2003), whereas the QTL detected on chromosome 22 for leg bone proportion is coincident with a QTL for HCW described by Kim et al. (2003). The same region on chromosome 16 that was linked to a pregrowth rate QTL in our study was found to be associated with preweaning ADG, HCW, and age-adjusted weaning weight (180-d BW) in a Wagyu × Limousin cross population (Alexander et al., 2007). The QTL detected on chromosome 22 for marbling is of particular interest, even though it did not have genome-wide significance, because it coincides with a QTL for intramuscular fat identified in the same population (Gutiérrez-Gil et al., 2008). Further study is needed to determine whether one or more causative genes underlie the coincident QTL identified in the different populations.

In conclusion, several highly significant and suggestive QTL were identified affecting in vivo and postmortem traits of importance for the beef industry. Several of these are new QTL regions, whereas some others are coincident with previously reported QTL. By including in our analysis a wide range of traits, especially those related to the full tissue dissection, our results shed light on the biological mechanisms underlying the effects identified by this and other studies. The information presented here serves as the starting point to identify markers that can be used in marker-assisted selection programs and for the identification of the trait-associated genes. The newly available bovine genome sequence and resulting genomic tools will be of great value to accomplish this objective. For the chromosome 6 QTL, various positional or functional, or both, candidate genes are discussed here, which could be tested directly for quantitative trait nucleotides affecting the traits. For those QTL in which alternative alleles appear to be carried by the 2 founder breeds, our results also contribute to identification of the genetic variation that underlies the differences between the Charolais and Holstein breeds.

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